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Increase in heterogeneity of biceps brachii activation during isometric submaximal fatiguing contractions: a multichannel surface EMG study

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Staudenmann D, van Dieën JH, Stegeman DF, Enoka RM. Increase in heterogeneity of biceps brachii activation during isometric submaximal fatiguing contractions: a multichannel surface EMG study. *J Neurophysiol* 111: 984–990, 2014. First published December 11, 2013; doi:10.1152/jn.00354.2013.—The effects of fatigue emerge from the beginning of sustained submaximal contractions, as shown by an increase in the amplitude of the surface electromyogram (EMG). The increase in EMG amplitude is attributed to an augmentation of the excitatory drive to the motor neuron pool that, more importantly than increasing discharge rates, recruits additional motor units for the contraction. The aim of this study was to determine whether the spatiotemporal distribution of biceps brachii (BB) activity becomes more or less heterogeneous during a fatiguing isometric contraction sustained at a submaximal target force. Multiple electrodes were attached over the entire BB muscle, and principal component analysis (PCA) was used to extract the representative information from multiple monopolar EMG channels. The development of heterogeneity during the fatiguing contraction was quantified by applying a cluster algorithm on the PCA-processed EMG amplitudes. As shown previously, the overall EMG amplitude increased during the sustained contraction, whereas there was no change in coactivation of triceps brachii. However, EMG amplitude did not increase in all channels and even decreased in some. The change in spatial distribution of muscle activity varied across subjects. As found in other studies, the spatial distribution of EMG activity changed during the sustained contraction, but the grouping and size of the clusters did not change. This study showed for the first time that muscle activation became more heterogeneous during a sustained contraction, presumably due to a decrease in the strength of common inputs with the recruitment of additional motor units.

electromyography; monopolar signals; muscle fatigue; principal component analysis; cluster algorithm; motor control

THE EFFECTS OF FATIGUE EMERGE from the beginning of sustained submaximal muscle contractions (Mosso 1906) as indicated by the increase of the amplitude of the surface electromyogram (EMG) needed to sustain the required force (Bigland and Lippold 1954; Cobb and Forbes 1923; De Luca 1984; Edwards and Lippold 1956). Because the motor units recruited from the beginning of a fatiguing contraction exhibit a progressive decrease in discharge rate (Mottram et al. 2005; Rudroff et al. 2011), the increase in EMG amplitude is generally attributed to the recruitment of additional motor units (Enoka et al. 2011; Gandevia 2001) but can also be influenced by changes in the conduction velocity of motor unit action potentials and the synchronization of motor unit discharge times (Arabadzhiev et al. 2010; Yao et al. 2000). Although the newly recruited motor units will initially increase discharge rate, they, too, will eventually reduce discharge rate, and additional motor units will be recruited (Carpentier et al. 2001).

Multichannel and intramuscular EMG studies have shown that muscle activity can show some spatial variability during brief muscle contractions (Falla and Farina 2007b; Farina et al. 2008; Hedayatpour et al. 2008; Holtermann et al. 2008; Staudenmann et al. 2009, 2013; ter Haar Romeny et al. 1984; van Zuylen et al. 1988) and that activity can alternate within a muscle during sustained and repetitive contractions (Sirin and Patla 1987; van Dieën et al. 1993). With the progressive recruitment of the motor unit pool during a sustained submaximal contraction, however, it can be expected that the distribution of surface EMG amplitudes would become more homogeneous as motor units with larger territories are recruited (Milner-Brown and Stein 1975). Such a prediction is based on the recognition that surface EMG recordings represent the linear addition of muscle fiber action potentials (Day and Hulliger 2001) and that motor unit size increases with motor unit recruitment threshold (Duchateau and Enoka 2011; Heckman and Enoka 2012). Although high-density EMG grids have demonstrated changes in the spatial distribution of muscle activity during fatiguing contractions (Falla and Farina 2007b; Farina et al. 2008; Hedayatpour et al. 2008; Holtermann et al. 2008), it remains unclear whether the spatial distribution becomes more or less heterogeneous as the contraction progresses. The findings to date, however, have not characterized the changes in the spatial distribution of the entire muscle due to limitations in the size of the high-density EMG grids. Moreover, multiple bipolar EMG recordings provide less accurate estimates of muscle activity compared with processing the same monopolar channels with principal component analysis (PCA; Staudenmann et al. 2006, 2013). It is expected that the active motor units within a muscle are represented with a higher accuracy when processing multiple monopolar EMG with PCA (cf. Staudenmann et al. 2010).

The aim of this study examined whether the spatiotemporal distribution of muscle activity in biceps brachii (BB) becomes more or less heterogeneous during a fatiguing isometric contraction sustained at a submaximal target force. Muscle activity was characterized with multiple surface electrodes distributed

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over the entire muscle (cf. Staudenmann et al. 2013). Monopolar EMG signals were processed with PCA to obtain more representative spatial information of the entire muscle activity (Staudenmann et al. 2006). A cluster algorithm was used to quantify the spatial distribution of muscle activity during the fatiguing contraction (cf. Staudenmann et al. 2009). Changes in consistency of EMG amplitude within and between clusters were tracked over time.

METHODS

Subjects and procedures. Ten healthy men (mean ± SD: age, 27.3 ± 8.3 yr; mass, 82.5 ± 12.8 kg; height, 1.8 ± 0.7 m), who reported no neurological or cardiovascular disorders, participated in the experiment. Informed, written consent was obtained before participation in the study. The Human Subjects Committee at the University of Colorado Boulder approved the protocol.

Subjects were prepared for the experiment and were seated in the experimental setup as described in a previous study (Staudenmann et al. 2013). Before the fatiguing contraction, each subject performed a maximum voluntary contraction (MVC) with the elbow flexor muscles by gradually increasing the force from rest to maximum, sustaining the maximum force for ~3 s, and then decreasing the force back to baseline. MVCs were repeated three times, and subjects were verbally encouraged to produce a maximal effort. The fatiguing contraction involved matching a target force set at 20% MVC force and sustaining the isometric contraction for one-half of the endurance limit as estimated from a Borg scale (Borg 1982); that is, the time until perceived fatigue reached one-half of the maximal value. The sustained contraction was limited to one-half of endurance time because this is a sufficient duration to detect significant changes in the activity of motor units in BB (Mottram et al. 2005) without the task being compromised by substantial challenges to homeostasis.

Mechanical recording. Subjects were seated upright in a chair with the left upper arm vertical, the forearm horizontal and in a neutral posture (midway between supination-pronation), and the elbow joint flexed to a right angle. The elbow was supported on a pad that restrained arm movements. The forearm was tightly fixed in a wrist-hand-thumb orthosis (Orthomerica, Newport Beach, CA) that was attached to a force transducer (force-moment sensor; JR3, Woodland, CA) to measure the upward force at the wrist. The orientation of the upper arm and forearm was aligned with the principal axes of the force transducer such that an elbow flexion moment mainly produced a force in upward direction. The normalized flexion force of 20% MVC was displayed as a horizontal line on a screen (resolution: 1% MVC per centimeter) that was located 1 m in front of the subject, and the force signal was recorded using a Power1401 analog-to-digital converter (1,000 samples per second, 12-bit resolution) and Spike2 software (version 5.02; Cambridge Electronic Design, Cambridge, United Kingdom).

Electrophysiological recording. Surface EMG was recorded from BB and from an antagonist muscle, the triceps brachii. Soft-E Repositionable Cloth Series Electrodes (H69P; Kendall, Boston, MA) were adapted by cutting away the material around the metallic clipper connection to obtain small electrodes (Ø ~0.8 cm). Recordings were obtained from 63 ± 4 electrodes that were attached over the BB of the 10 subjects. The 1st electrode was placed over the intersection of the innervation zone (halfway between proximal and distal edges of BB; see Masuda et al. 1983), and the septum between the BB muscle heads, which was determined by palpation. The electrodes were then added in medial and lateral directions with an interelectrode distance of 1.5 cm until the edges of BB were reached. Parallel to the first row over the innervation zone, proximal and distal rows of electrodes were added with the same interelectrode distance resulting in evenly spaced electrodes placed over the entire BB (Fig. 1). Furthermore, one pair of bipolar electrodes was attached over each of the long and lateral heads of triceps brachii with 1.5 cm between the electrodes. The reference electrode was placed over the lateral epicondyle of the elbow. The electrodes were connected to the amplifier (Refa; TMSi, Oldenzaal, The Netherlands) and processed as monopolar EMG signals (input impedance $>10^{12}$ Ω, internal antialiasing filter at 400 Hz, analog-to-digital conversion at 2,000 samples per second, 24-bit resolution).

Data analysis. The data were analyzed with MATLAB (The MathWorks, Natick, MA). Force signals were upsampled (using cubic spline interpolation) and aligned to the EMG signals with a synchronization pulse. The data were segmented into three 10-s time windows: start, middle, and end (Fig. 1). The standard deviation of force was determined in each time window. The EMG recordings from both BB and triceps brachii were high-pass filtered (10-Hz, Butterworth, 1st-order, bidirectional). The monopolar BB signals were then subjected to PCA, which acts as spatial filter and substantially improves the estimation of muscle activation compared with bipolar recordings

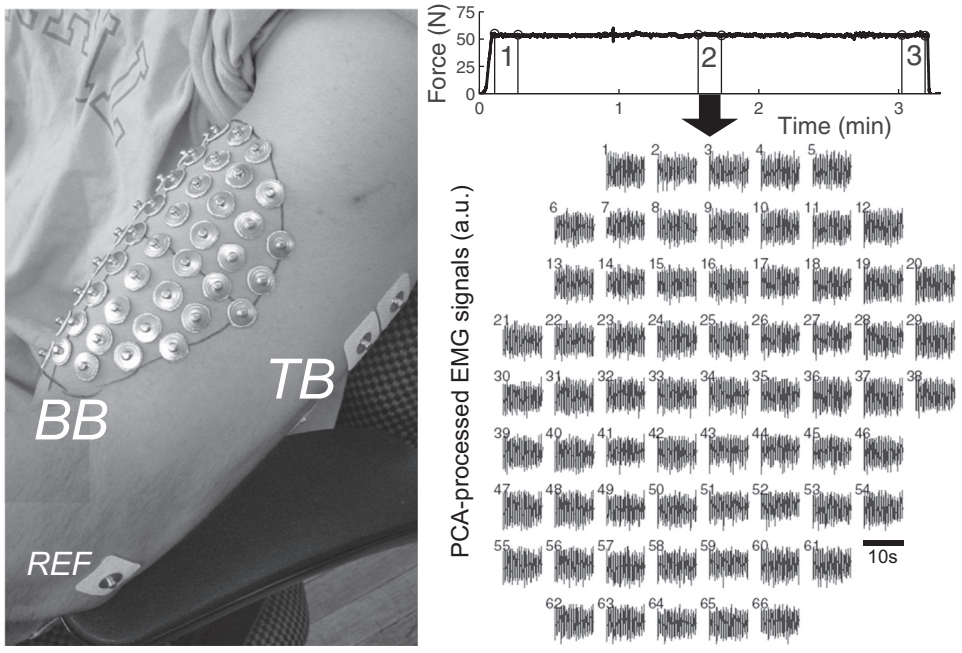

Fig. 1. The electrode coverage over the biceps brachii (BB) muscle for 1 subject. The *right top* shows the force exerted (~54 N) during the isometric contraction with 3 10-s time windows (vertical lines) indicated at the start, middle, and end of the contraction. Sixty-six electrodes were attached over BB for this subject, which resulted in 66 principal component analysis (PCA)-processed electromyographic (EMG) signals, shown in arbitrary units (a.u.) fluctuating around 0. Single bipolar electrodes were attached over the long and lateral heads of triceps brachii (TB). The reference electrode (REF) was attached over the lateral aspect of the elbow.

(Staudenmann et al. 2006, 2013). This improvement was achieved by discarding the 1st 4 principal components (PCs; Staudenmann et al. 2013), which is realized by summing the 5th to the last PC (vector multiplication of: time series, relative distribution; cf. Staudenmann et al. 2006) and is denoted as the PCA-processed EMG amplitude throughout the article (Fig. 1). The 1st 4 components were discarded to minimize the influence of signals that arise from distant sources, which is similar to obtaining a differential recording with bipolar electrodes. Moreover, the use of PCA on monopolar recordings reduces the confounding influence of electrode placement relative to the orientation of the muscle fibers (cf. Staudenmann et al. 2010). A single bipolar signal was derived for each of the two heads of triceps brachii. Subsequently, all EMG signals were rectified and smoothed (1-Hz, Butterworth, 1st-order, bidirectional). The mean ± SD of the EMG amplitude was determined for all BB channels in each time window. The same analysis was applied to the averaged EMG amplitude over 2 heads of triceps brachii to obtain an index of coactivation.

A *k*-means cluster algorithm was applied to identify distinct clusters of PCA-processed EMG amplitudes within BB. In the *k*-means algorithm, correlation was used as a distance measure to characterize covariance of activity within BB. The number of clusters was arbitrarily set to five. Briefly, the cluster algorithm allocates channels to a cluster (here based on the intracluster correlation coefficient of the PCA-processed EMG amplitudes) and generates a representative wave shape for each cluster (for further information, see Staudenmann et al. 2009). The clusters were ranked based on the number of channels per cluster in decreasing order. Then, the degree of spatial dispersion of the channels belonging to one cluster was determined for each cluster. To this end, the spatial distance between each pair of electrodes within a cluster was estimated and averaged to obtain a single distance value. The same distance was calculated for a hypothetical maximally grouped cluster with the same number of channels. The degree of spatial clustering (in percentage) was estimated by dividing maximally grouped by measured distance. The value declines as the channels are scattered over BB. The degree of heterogeneity in BB muscle activity was quantified by determining the correlation coefficients among channels for the wave shapes within and between clusters.

Statistics. The results were analyzed with repeated-measures ANOVA (sphericity assumed, using SPSS, Chicago, IL) with significance set at 5%. The following dependent variables were examined with time window as a fixed factor: standard deviation of force; PCA outcome (1st PC; sum of 5th to last PC); overall PCA-processed EMG amplitude (mean and SD) for BB and a mean bipolar EMG amplitude for triceps brachii; size and grouping of the clusters; and the correlation coefficient (after Fisher *z*-transformation) of channels within and between cluster time series. The data subjected to ANOVA showed equal variance as indicated by Mauchly's test of sphericity.

RESULTS

Mechanical recording. The 20% MVC flexion force was sustained at 61.2 ± 7.5 N (torque 17.4 ± 1.9 Nm) until subjects reached one-half of the endurance limit, which resulted in the contraction lasting 2.74 ± 1.30 min. The perceived fatigue estimated from the Borg scale (1–10) for the three time windows were 1.4 ± 1.0 for the start, 3.2 ± 0.7 for the middle, and 5.0 ± 0.0 (by definition) for the end. The standard deviation for force (0.098 ± 0.029 N) showed no significant effect of time window ($P = 0.848$).

PCA of multiple monopolar EMG channels. The relative contribution of the first PC was significantly different between time windows ($P = 0.001$). Post hoc analysis showed a slight decrease of ~3%, from 83.4 ± 8.8% in the first time window ($P = 0.005$) to an average of 80.5 ± 8.9% for the remaining two time windows (*2-3*), which did not differ significantly ($P = 0.12$). The relative contributions of the remaining PCs (5th until last PC; used to estimate muscle activity) showed an opposite significant effect of time window ($P = 0.013$). However, post hoc analysis showed no significant effect starting at 5.8 ± 4.1% (*1-2*: $P = 0.061$) and increasing to an average of 8.2 ± 5.0% for the 2 last time windows ($P = 0.260$).

EMG amplitudes and standard deviation. Based on the PCA-processed EMG signals, the average amplitude differed significantly between time windows ($P < 0.001$), with an increase of 25% between the first and second window ($P < 0.001$) and no significant difference between the last two time windows ($P = 0.118$; Fig. 2). The variability (standard deviation) of the EMG amplitude over the time window was not significantly different between time windows ($P = 0.683$). However, individual subjects showed quite variable patterns of spatiotemporal changes in EMG amplitudes across the time windows, especially the first two time windows (Fig. 3). The average and the standard deviation of the EMG amplitude of the antagonist muscle triceps brachii (143 ± 70 μV) did not change across the three time windows ($P > 0.108$).

Clusters of multiple EMG amplitudes within BB. The PCA-processed EMG amplitudes over BB showed different spatial patterns (Fig. 4) as represented by the cluster outcomes (Fig. 5). Across the 10 subjects, the 5 clusters comprised

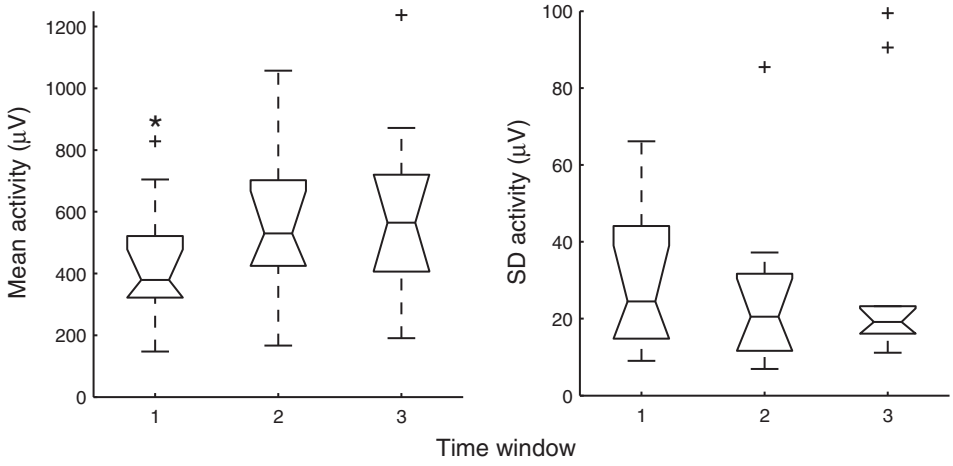

Fig. 2. Mean amplitudes of the PCA-processed EMG signals as estimated over all BB recordings for the 3 time windows (*1–3*) during the fatiguing contraction. The *left* shows the mean overall BB recordings, and the *right* shows the standard deviation of the EMG amplitude for BB. Box plots show the results for all subjects; the middle line in each box plot represents the median value, and the error bars indicate the range. The *bottom* and *top* limits of each box represent the interquartile range, and the plus signs denote outliers. Note the significant (*) increase in mean EMG amplitude after the 1st time window.

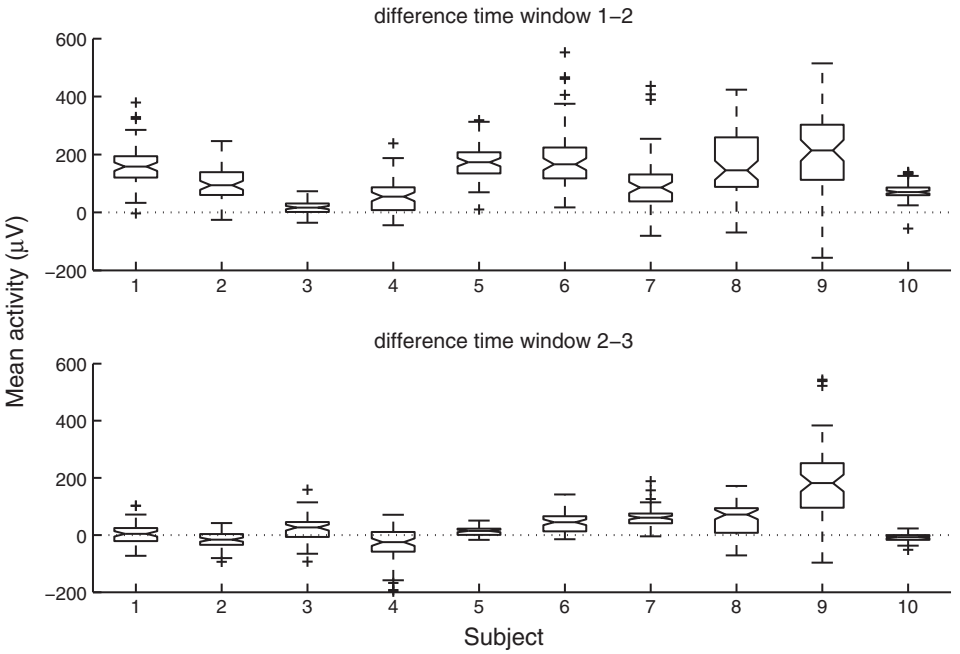

Fig. 3. Difference in PCA-processed EMG amplitudes between consecutive time windows for the 10 subjects. The *top* shows the differences in EMG amplitudes for all BB channels between *time windows 1* and *2*, and the *bottom* shows the differences between *time windows 2* and *3*. The middle line in each box represents the median value, and the error bars indicate the range. The lower and upper limits for each box represent the interquartile range, and the plus signs denote outliers. Note that although on average EMG amplitudes increased during the 1st half of the contraction, some EMG channels detected a decrease in EMG amplitude as indicated by the error bars crossing the 0 line.

31.9 ± 5.4, 25.6 ± 4.4, 18.7 ± 3.1, 14.1 ± 3.9, and 9.7 ± 4.0% of the total number of EMG channels from the largest to the smallest cluster. These percentages did not differ between time windows ($P = 0.527$). Moreover, the distribution of channels belonging to the same cluster (Fig. 5) indicates that the grouping of clusters did not differ between time windows ($P = 0.569$). Correlation coefficients between channels within and between clusters both decreased significantly after the first time window ($P < 0.017$), whereas there were no further significant changes between the last two time windows ($P > 0.457$). Figure 6 indicates that the correlations within clusters were on average 31% greater ($r = 0.61 \pm 0.17$) than the correlations between clusters ($r = 0.42 \pm 0.30$). There was a 20% reduction ($r = 0.70 \pm 0.08$, $r = 0.56 \pm 0.13$) for the within-cluster correlations and a 38% reduction ($r = 0.57 \pm 0.14$, $r = 0.34 \pm 0.09$) for the between-cluster correlations comparing the first time window with the subsequent time windows.

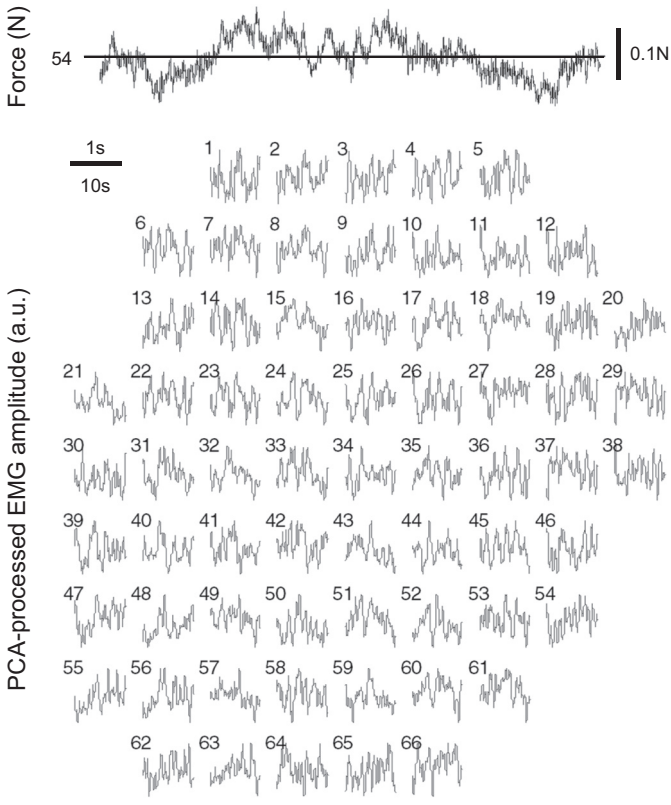

Fig. 4. An example of force (*top* trace, expanded view with 1-s calibration) and EMG signals for the middle 10-s time window of the fatiguing contraction (same subject as in Fig. 1) sustained at ~54 N. The numbered traces in the *bottom* show the spatiotemporal pattern of the PCA-processed EMG amplitude after rectification and smoothing over the entire BB. These EMG amplitudes were used as input to the cluster algorithm. Note the temporal and spatial variability of the EMG amplitude despite a relatively constant force.

DISCUSSION

The current study examined whether the spatiotemporal distribution of muscle activity in BB became more or less heterogeneous during an isometric contraction at a submaximal target force with the elbow flexor muscles. As observed in previous studies using high-density EMG recordings, the spatial distribution of muscle activity changes during the fatiguing contraction (Falla and Farina 2007b; Farina et al. 2008; Hedayatpour et al. 2008; Holtermann et al. 2008). The new finding in the current study was that the spatial distribution of muscle activity became more heterogeneous during the first part of the fatiguing contraction and then stabilized (Fig. 6). It was possible to detect this profile of adjustments by acquiring multiple monopolar EMG recordings over the entire muscle and processing the data with PCA, which provide superior quality of muscle activity estimates compared with multiple bipolar EMG recordings over BB (Staudenmann et al. 2013). It is expected that the active motor units within a muscle are represented with a higher accuracy when processing multiple monopolar EMG with PCA (cf. Staudenmann et al. 2010). The current study is the first to apply PCA to monopolar EMG

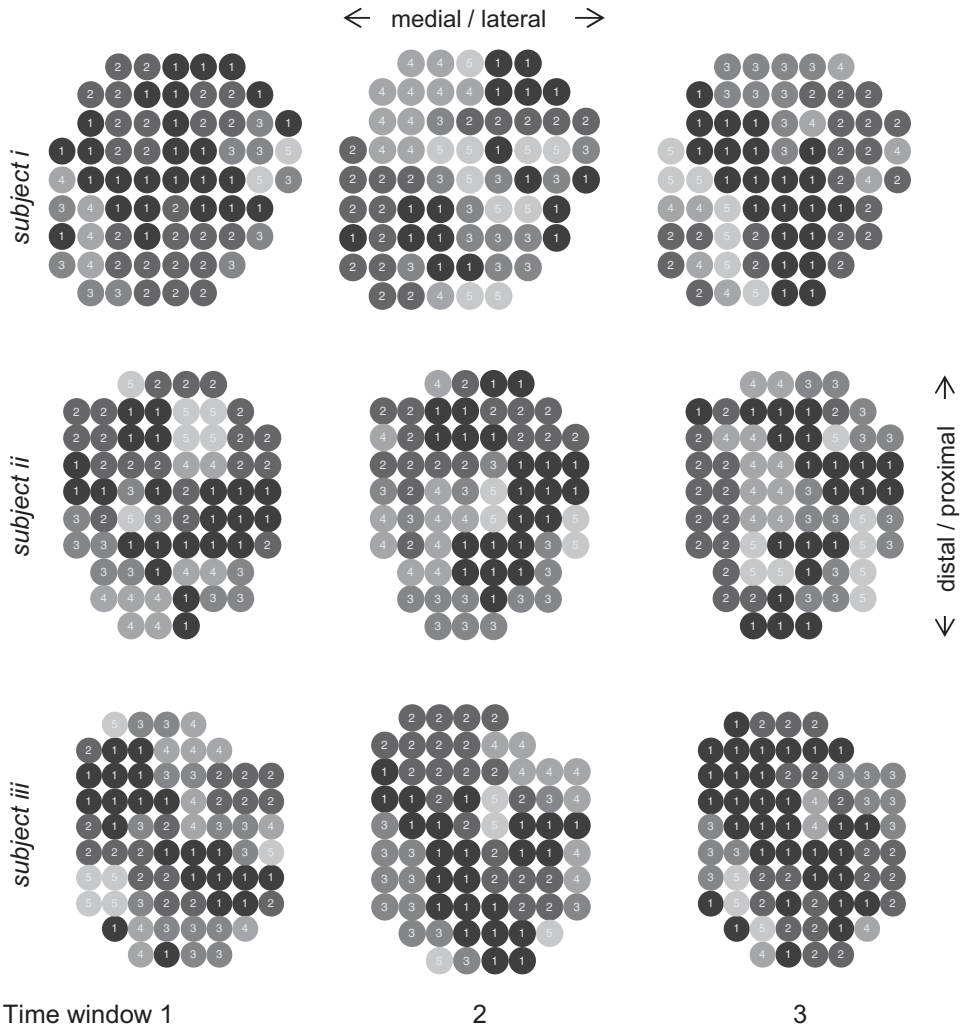

Fig. 5. Example of 3 representative subjects (*subject i*, same subject as in Fig. 1) showing the clusters obtained for the 3 time windows (start, middle, and end of the contraction). By definition, *cluster 1* is the largest (numbers inside the circles), and *cluster 5* the smallest. Channels within clusters were spread over the entire muscle and showed no specific grouping within the anatomically distinct muscle heads.

signals to characterize the adjustments in muscle activity during a sustained submaximal contraction.

The results in the current study are consistent with prior reports showing an increase in the surface EMG amplitude during fatiguing contractions (Cobb and Forbes 1923; Edwards and Lippold 1956; Fuglevand et al. 1993; Lind and Petrofsky 1979; Rudroff et al. 2008) and the absence of an increase in coactivation of the triceps brachii muscle (cf. Levenez et al. 2005; Maluf and Enoka 2005). Figure 2 indicates that the average amplitude over a window of the PCA-processed EMG signals for BB increased by 25% from the first to the second time window but then did not increase any further as the contraction was sustained up to one-half of the estimated endurance limit. Although there was an increase in the overall EMG amplitude, it did not increase in all EMG channels over BB. The error bars in Fig. 3, *top*, indicate that some channels even exhibited a reduction in EMG amplitude, which has also been observed by others (De Luca 1984; Dimitrova and Dimitrov 2003; Fitts 1994). The spatial variability of changes in the EMG amplitudes over the BB indicates spatiotemporal differ-

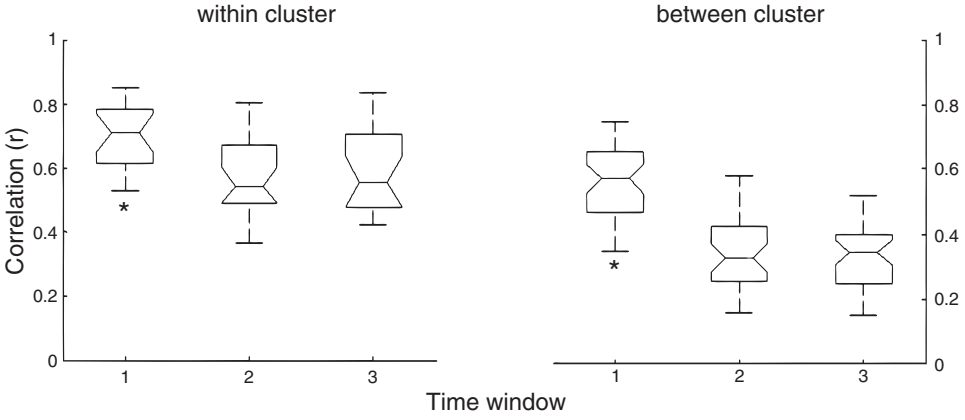

Fig. 6. Overall results for the cluster correlations between EMG channels across the 3 time windows (*1–3*). *Left* shows the distribution over subjects of the mean correlations for the time series within clusters, and the *right* shows the distributions of the correlations of the representative wave shapes between clusters. The middle line in each box represents the median value, and the error bars indicate the range. The lower and upper limits for each box represent the interquartile range, and the plus signs denote outliers. Note the higher correlation within clusters compared with between clusters and the significant drop in correlation (*) after the 1st time window for the between-clusters time series.

ences between subjects (Fig. 5), and, as found in other studies during brief isometric contractions, changes in the overall EMG amplitude were not representative of the activity for the entire muscle (Falla and Farina 2007a; Holtermann et al. 2008; Staudenmann et al. 2009, 2013; van Zuylen et al. 1988).

The spatial distribution of muscle activity, as indicated by the arrangement of the clusters over the BB, changed over time during the sustained contraction (Fig. 5), again as shown previously (e.g., Falla and Farina 2007b; Farina et al. 2008; Holtermann et al. 2008). Channels within clusters were spread over the entire muscle and showed no specific grouping even within the anatomically distinct long and short heads of BB (cf. van Zuylen et al. 1988). There were no systematic changes during the sustained contraction in the current study in either the degree of spatial grouping or the number of channels per cluster. Previous work on triceps surae muscle also indicated no obvious anatomical interpretation of the functionally derived clusters for the individual muscles during a nonfatiguing contraction (Staudenmann et al. 2009). Further results showed that after the first time window there was a substantial increase in the heterogeneity of BB activation as evidenced by a decrease in the correlation coefficients among the channels within a cluster (20%) and an even larger decrease of the correlation coefficients between the cluster time series (38%).

Although the discharge rates of BB motor units decline progressively and additional motor units are recruited during isometric contractions sustained at the same relative target force for a similar duration, EMG amplitude as estimated from bipolar recording increased modestly (~5%) during the sustained contraction (Mottram et al. 2005; Rudroff et al. 2010). In apparent contradiction, the adjustments in EMG amplitudes in the current study were only observed during the first half of the sustained isometric contraction. Consistent with this result, however, a computational model of motor unit recruitment and rate coding during a comparable fatiguing contraction also predicted that EMG amplitude increases initially and then remains constant (Dideriksen et al. 2011). The most likely explanation for the discrepancy is that bipolar EMG recordings provide a limited estimate of muscle activation (Farina et al. 2004) compared with multiple PCA-processed monopolar EMG signals over the entire muscle (Staudenmann et al. 2006, 2013). Thus the current findings provide a more accurate estimate of the adjustments in motor unit activity in BB during the sustained submaximal contraction.

Given that the coactivation of triceps brachii did not increase in the current study and that the overall EMG amplitude increased initially and then plateaued, the progressive increase in the rating of perceived contraction must have been driven by an increase in activity of the synergist muscles. In a similar experimental setup, the activation among elbow flexors, at least as measured with surface bipolar recordings, differed during fatiguing contractions (Hunter et al. 2003), and different rates of increase in EMG amplitude were observed between elbow flexor muscles when measuring surface and intramuscular EMG (Rudroff et al. 2008). Consequently, the target force must have been sustained for the prescribed duration by a nonuniform increase in activation across the muscles that contributed to the net elbow flexor torque (Buchanan et al. 1986) as the coordination among synergists can attenuate the decline in force capacity during a fatiguing contraction (Dul et al. 1984; Kouzaki and Shinohara 2006). Nonetheless, an increase in the heterogeneity of the spatiotemporal distribution of BB muscle activity, as observed in the current study, is likely related to the adjustments in activity across the involved muscles (cf. van Zuylen et al. 1988).

The progressive recruitment of motor units with greater innervation numbers should increase the homogeneity of EMG activity (cf. De Luca et al. 1993). In contrast, the current results indicated that the distribution of PCA-processed EMG amplitudes became heterogeneous during the first part of the sustained contraction and then stabilized. Similarly, a computational model predicts that the largest motor units are not recruited until much later during an isometric contraction sustained at the same intensity (20% MVC) as in the current study (Dideriksen et al. 2011), which suggests that the initial increase in heterogeneity is unlikely due to the progressive recruitment of larger motor units.

Although motor unit synchronization can cause an increase in EMG amplitude (Yao et al. 2000), our results showed an increase in EMG amplitude that was accompanied by an increase and not a decrease in heterogeneity (comparing Figs. 2 and 6, respectively). Furthermore, the change in heterogeneity did not covary with the force fluctuations, which was associated with the strength of motor unit synchronization (cf. Semmler and Nordstrom 1998). Moreover, a computational model demonstrated that the imposition of motor unit synchronization causes a peak between 16 and 32 Hz in the coherence spectrum derived from the discharge times of pairs of motor units (Moritz et al. 2005). The increase of heterogeneity of the spatiotemporal distribution of BB muscle activity, therefore, likely indicates a decrease in the strength of common input associated with motor unit synchronization. It remains to be determined whether the heterogeneity of muscle activity increases in longer-duration contractions when larger motor units are recruited and the number of motor unit action potentials increases as task failure approaches.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

D.S., J.H.v.D., D.F.S., and R.M.E. conception and design of research; D.S. performed experiments; D.S. analyzed data; D.S., J.H.v.D., D.F.S., and R.M.E. interpreted results of experiments; D.S. prepared figures; D.S. drafted manuscript; D.S., J.H.v.D., D.F.S., and R.M.E. edited and revised manuscript; D.S., J.H.v.D., D.F.S., and R.M.E. approved final version of manuscript.

REFERENCES

Arabadzhiev TI, Dimitrov VG, Dimitrova NA, Dimitrov GV. Interpretation of EMG integral or RMS and estimates of "neuromuscular efficiency" can be misleading in fatiguing contraction. *J Electromyogr Kinesiol* 20: 223–232, 2010.

Bigland B, Lippold OC. Motor unit activity in the voluntary contraction of human muscle. *J Physiol* 125: 322–335, 1954.

Borg GA. Psychophysical bases of perceived exertion. *Med Sci Sports Exerc* 14: 377–381, 1982.

Buchanan TS, Almdale DP, Lewis JL, Rymer WZ. Characteristics of synergic relations during isometric contractions of human elbow muscles. *J Neurophysiol* 56: 1225–1241, 1986.

Carpentier A, Duchateau J, Hainaut K. Motor unit behaviour and contractile changes during fatigue in the human first dorsal interosseus. *J Physiol* 534: 903–912, 2001.

Cobb S, Forbes A. Electromyography studies of muscle fatigue in man. *Am J Physiol* 65: 234–251, 1923.

Day SJ, Hulliger M. Experimental simulation of cat electromyogram: evidence for algebraic summation of motor-unit action-potential trains. *J Neurophysiol* 86: 2144–2158, 2001.

De Luca CJ. Myoelectrical manifestations of localized muscular fatigue in humans. *Crit Rev Biomed Eng* 11: 251–279, 1984.

De Luca CJ, Roy AM, Erim Z. Synchronization of motor-unit firings in several human muscles. *J Neurophysiol* 70: 2010–2023, 1993.

Dideriksen JL, Enoka RM, Farina D. Neuromuscular adjustments that constrain submaximal EMG amplitude at task failure of sustained isometric contractions. *J Appl Physiol* 111: 485–494, 2011.

Dimitrova NA, Dimitrov GV. Interpretation of EMG changes with fatigue: facts, pitfalls, and fallacies. *J Electromyogr Kinesiol* 13: 13–36, 2003.

Duchateau J, Enoka RM. Human motor unit recordings: origins and insight into the integrated motor system. *Brain Res* 1409: 42–61, 2011.

Dul J, Johnson GE, Shiavi R, Townsend MA. Muscular synergism–II. A minimum-fatigue criterion for load sharing between synergistic muscles. *J Biomech* 17: 675–684, 1984.

Edwards RG, Lippold OC. The relation between force and integrated electrical activity in fatigued muscle. *J Physiol* 132: 677–681, 1956.

Enoka RM, Baudry S, Rudroff T, Farina D, Klass M, Duchateau J. Unraveling the neurophysiology of muscle fatigue. *J Electromyogr Kinesiol* 21: 208–219, 2011.

Falla D, Farina D. Motor units in cranial and caudal regions of the upper trapezius muscle have different discharge rates during brief static contractions. *Acta Physiol (Oxf)* 192: 551–558, 2007a.

Falla D, Farina D. Periodic increases in force during sustained contraction reduce fatigue and facilitate spatial redistribution of trapezius muscle activity. *Exp Brain Res* 182: 99–107, 2007b.

Farina D, Leclerc F, Arendt-Nielsen L, Buttelli O, Madeleine P. The change in spatial distribution of upper trapezius muscle activity is correlated to contraction duration. *J Electromyogr Kinesiol* 18: 16–25, 2008.

Farina D, Merletti R, Enoka RM. The extraction of neural strategies from the surface EMG. *J Appl Physiol* 96: 1486–1495, 2004.

Fitts RH. Cellular mechanisms of muscle fatigue. *Physiol Rev* 74: 49–94, 1994.

Fuglevand AJ, Zachowski KM, Huey KA, Enoka RM. Impairment of neuromuscular propagation during human fatiguing contractions at submaximal forces. *J Physiol* 460: 549–572, 1993.

Gandevia SC. Spinal and supraspinal factors in human muscle fatigue. *Physiol Rev* 81: 1725–1789, 2001.

Heckman CJ, Enoka RM. Motor unit. *Compr Physiol* 2: 2629–2682, 2012.

Hedayatpour N, Arendt-Nielsen L, Farina D. Non-uniform electromyographic activity during fatigue and recovery of the vastus medialis and lateralis muscles. *J Electromyogr Kinesiol* 18: 390–396, 2008.

Holtermann A, Gronlund C, Karlsson JS, Roeleveld K. Differential activation of regions within the biceps brachii muscle during fatigue. *Acta Physiol (Oxf)* 192: 559–567, 2008.

Hunter SK, Lepers R, MacGillis CJ, Enoka RM. Activation among the elbow flexor muscles differs when maintaining arm position during a fatiguing contraction. *J Appl Physiol* 94: 2439–2447, 2003.

Kouzaki M, Shinohara M. The frequency of alternate muscle activity is associated with the attenuation in muscle fatigue. *J Appl Physiol* 101: 715–720, 2006.

Levenez M, Kotzamanidis C, Carpentier A, Duchateau J. Spinal reflexes and coactivation of ankle muscles during a submaximal fatiguing contraction. *J Appl Physiol* 99: 1182–1188, 2005.

Lind AR, Petrofsky JS. Amplitude of the surface electromyogram during fatiguing isometric contractions. *Muscle Nerve* 2: 257–264, 1979.

Maluf KS, Enoka RM. Task failure during fatiguing contractions performed by humans. *J Appl Physiol* 99: 389–396, 2005.

Masuda T, Miyano H, Sadoyama T. The distribution of myoneural junctions in the biceps brachii investigated by surface electromyography. *Electroencephalogr Clin Neurophysiol* 56: 597–603, 1983.

Milner-Brown HS, Stein RB. The relation between the surface electromyogram and muscular force. *J Physiol* 246: 549–569, 1975.

Moritz CT, Christou EA, Meyer FG, Enoka RM. Coherence at 16–32 Hz can be caused by short-term synchrony of motor units. *J Neurophysiol* 94: 105–118, 2005.

Mosso A. *Fatigue*. London: Swan Sonnenschein, 1906.

Mottram CJ, Jakobi JM, Semmler JG, Enoka RM. Motor-unit activity differs with load type during a fatiguing contraction. *J Neurophysiol* 93: 1381–1391, 2005.

Rudroff T, Jordan K, Enoka JA, Matthews SD, Baudry S, Enoka RM. Discharge of biceps brachii motor units is modulated by load compliance and forearm posture. *Exp Brain Res* 202: 111–120, 2010.

Rudroff T, Justice JN, Holmes MR, Matthews SD, Enoka RM. Muscle activity and time to task failure differ with load compliance and target force for elbow flexor muscles. *J Appl Physiol* 110: 125–136, 2011.

Rudroff T, Staudenmann D, Enoka RM. Electromyographic measures of muscle activation and changes in muscle architecture of human elbow flexors during fatiguing contractions. *J Appl Physiol* 104: 1720–1726, 2008.

Semmler JG, Nordstrom MA. Motor unit discharge and force tremor in skill- and strength-trained individuals. *Exp Brain Res* 119: 27–38, 1998.

Sirin AV, Patla AE. Myoelectric changes in the triceps surae muscles under sustained contractions. Evidence for synergism. *Eur J Appl Physiol Occup Physiol* 56: 238–244, 1987.

Staudenmann D, Kingma I, Daffertshofer A, Stegeman DF, van Dieën JH. Heterogeneity of muscle activation in relation to force direction: a multichannel surface electromyography study on the triceps surae muscle. *J Electromyogr Kinesiol* 19: 882–895, 2009.

Staudenmann D, Kingma I, Daffertshofer A, Stegeman DF, van Dieën JH. Improving EMG-based muscle force estimation by using a high-density EMG grid and principal component analysis. *IEEE Trans Biomed Eng* 53: 712–719, 2006.

Staudenmann D, Roeleveld K, Stegeman DF, van Dieën JH. Methodological aspects of SEMG recordings for force estimation–a tutorial and review. *J Electromyogr Kinesiol* 20: 375–387, 2010.

Staudenmann D, Stegeman DF, van Dieën JH. Redundancy or heterogeneity in the electric activity of the biceps brachii muscle? Added value of PCA-processed multi-channel EMG muscle activation estimates in a parallel-fibered muscle. *J Electromyogr Kinesiol* 23: 892–898, 2013.

ter Haar Romeny BM, van der Gon JJ, Gielen CC. Relation between location of a motor unit in the human biceps brachii and its critical firing levels for different tasks. *Exp Neurol* 85: 631–650, 1984.

van Dieën JH, Oude Vrielink HH, Toussaint HM. An investigation into the relevance of the pattern of temporal activation with respect to erector spinae muscle endurance. *Eur J Appl Physiol Occup Physiol* 66: 70–75, 1993.

van Zuylen EJ, Gielen CC, Denier van der Gon JJ. Coordination and inhomogeneous activation of human arm muscles during isometric torques. *J Neurophysiol* 60: 1523–1548, 1988.

Yao W, Fuglevand RJ, Enoka RM. Motor-unit synchronization increases EMG amplitude and decreases force steadiness of simulated contractions. *J Neurophysiol* 83: 441–452, 2000.